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The effects of time delay on the stochastic resonance in feed-forward-loop neuronal network motifs

Chen Liu [a], Jiang Wang [a,*], Haitao Yu [a], Bin Deng [a], K.M. Tsang [b], W.L. Chan [b], Y.K. Wong [b]

[a] Department of Electrical Engineering and Automation, Tianjin University, Tianjin, China
[b] Department of Electrical Engineering, The Hong Kong Polytechnic University, Kowloon, Hong Kong, China

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ABSTRACT

The dependence of stochastic resonance in the feed-forward-loop neuronal network motifs on the noise and time delay are studied in this paper. By computational modeling, Izhikevich neuron model with the chemical coupling is used to build the triple-neuron feed-forward-loop motifs with all possible motif types. Numerical results show that the correlation between the periodic subthreshold signal's frequency and the dynamical response of the network motifs is resonantly dependent on the intensity of additive spatiotemporal noise. Interestingly, the excitatory intermediate neuron could induce intermittent stochastic resonance, whereas the inhibitory one weakens its influence on the intermittent mode. More importantly, it is found that the increasing delays can induce the intermittent appearance of regions of stochastic resonance. Based on the effects of the time delay on the stochastic resonance, the reasons and conditions of such intermittent resonance phenomenon are analyzed.

1. Introduction

Noise is ubiquitous in both natural and engineered systems; its constructive role has been the subject of intensive studies for over a decade [1,2]. Especially, noise-induced complex dynamic behaviors such as stochastic resonance have been studied extensively in nonlinear dynamics [3–9]. Stochastic resonance is characterized by the optimal response of a nonlinear system to a weak external deterministic signal [10–14]. Notably, stochastic resonance has been extensively reported to exist in a wide variety of neuronal models [11,12,15,16]. Recently, Matjaž Perc et al. gave a detailed description of stochastic resonance on excitable small-world networks via a pacemaker. They showed that the correlation between the frequency of subthreshold pacemaker activity and the response of an excitable array is resonantly dependent on the intensity of additive spatiotemporal noise [17]. Additionally, further researches on stochastic resonance on weakly paced scale-free networks, diffusive networks and feed-forward neuronal networks of bistable oscillators show that an intermediate intensity of temporally and spatially uncorrelated noise can optimally assist the pacemaker in imposing its rhythm on the whole ensemble, thus, it provides evidence for stochastic resonance on weakly paced various types of the neuronal networks [18–20].

Recently, researches about the stochastic resonances on complex neuronal networks have attracted a great number of the attentions and the majority of previous researches deal with the dynamics of various complex neuronal system such as regular diffusively coupled networks [21,19], small-world networks [22] and scale-free networks [23,18,19]. Moreover, intensive statistical analysis has revealed that some significant recurring nontrivial patterns of interconnections, termed "network motifs," which are believed to be basic building blocks of various neuronal networks. Currently, network motifs are widely

* Corresponding author. Tel./fax: +86 22 27402293.
E-mail address: jiangwang@tju.edu.cn (J. Wang).

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studied on neuroscience and suggested to perform specific functional roles [24,25]. A number of systematic research works have demonstrated that these motifs do exist widely in real biological networks, especially, in neuronal networks [26–28] and brain functional networks [29] by mathematical and experimental research. Previous studies have found that the motifs which are linked to each other in a special way remain their own independent function of each motif [30]. It suggests that the network dynamics might be understood as combinations of these elementary computational units [31]. And thus, the dynamics and special functions of these network motifs can be treated as the first step to understand the behaviors of whole networks.

The triple-neuron feed-forward-loop (FFL) is one of the most important neuronal network motifs [28]. In Ref. [28], three neurons are significantly over-represented relative to the expectations based on the statistics of smaller inter-connectivity patterns, as shown in Fig. 1, where neuron 1 drives neuron 2 and neuron 3, and neuron 2 drives neuron 3. In this motif, neurons 1, 2 and 3 can be regarded as the input, intermediate and output neurons, respectively. In consideration of the fact that neurons can be divided into excitatory and inhibitory neurons, eight possible structural configurations are obtained, as shown in Table 1, where E and I are used to represent excitatory and inhibitory neurons, respectively. Excitatory neurons encourage neurons to act the activity, whereas inhibitory ones play an opposite role. Recently, Li et al. have studied stochastic and coherence resonance in FFL neuronal network motifs [32]. They demonstrated the FFL motifs are more significant than the other simple chain structure as given in Ref. [33]. By comparison the effects of the stochastic resonance in the eight structural configurations, they showed that all possible structures can induce the optimal stochastic resonance in weak-coupling regime. However, the work in [32] did not consider the effects of time delay.

In real neural systems, time delays that mainly originate from the finite speed of action potential propagating across neuron axons and time lapses occurring by both dendritic and synaptic processes are inevitable in intermediate neuronal communication and inherent to the nervous system. Typical conduction velocities are approximately equal to 10 m/s, leading to non-negligible information transmission times, in the order of milliseconds or even hundreds of milliseconds [17]. It is found that time delay can not only facilitate and improve neuronal synchronization [34–37], but also induce multi resonances [38–42] leading to many interesting phenomena [43–45]. Moreover, it has been shown that time delays through chemical synapses play subtle roles in firing transitions, e.g., in-phase synchronization and anti-phase synchronization can be induced by time delays in map-based small-world neuronal networks with hybrid synapses [46].

At present, this paper aims to use computational modeling to systemically explore the dependence of stochastic resonance on the information transmission delay and the different structural configurations over FFL neuronal network motifs. Results show that the delay-induced stochastic resonance of the coupled neuronal network motifs can appear intermittently. Multiple stochastic resonances can occur on the neuronal network motifs if the durations of the delays are appropriately tuned. Accordingly, the remainder of this paper is organized as follows. In Section 2, the Izhikevich neuron model with chemical coupling is introduced. Section 3 is devoted to report the simulation results on the stochastic resonance in the FFL neuronal network motifs. Finally, a brief discussion and conclusion of our work are given in Section 4.

2. Model and method

Combine the biologically plausibility of Hodgkin–Huxley type dynamics and the computational efficiency of integrate-and-fire neurons, the Izhikevich neuron model is used to build the FFL neuronal network motifs [47]. The dynamics of the studied motifs is governed by the following two equations:

$$\frac{dv_i}{dt} = 0.04v_i + 5v_i + 140 - u_i + I_i^{noise} + I_i^{syn} + I_i^{ext} \tag{1}$$

$$\frac{du_i}{dt} = a(bv_i - u_i) \tag{2}$$

with the auxiliary after-spike resetting

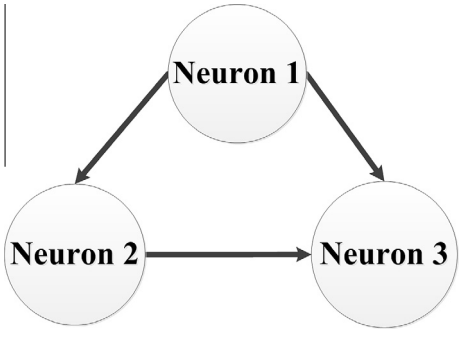

Fig. 1. Connection patterns of the FFL neuronal network motif: neuron 1 drives neuron 2, and both jointly drive neuron 3.

Table 1
Eight possible FFL types.

Type	Neuron 1	Neuron 2	Neuron 3
T1-FFL	E	E	E
T2-FFL	E	I	E
T3-FFL	E	E	I
T4-FFL	E	I	I
T5-FFL	I	E	E
T6-FFL	I	I	E
T7-FFL	I	E	I
T8-FFL	I	I	I

$$\text{if } v_i \geqslant 30\ \text{mV, then} \begin{cases} v_i = c \\ u_i = u_i + d \end{cases} \tag{3}$$

where $i = 1, 2, 3$ index the neurons, $dt = 0.1$ ms is a fixed integrated time step. v_i denotes the membrane potential of the neuron, u_i represents the membrane recovery variable, and a, b, c, d are four dimensionless parameters which are used to determine the neuron type. According to Ref. [47], the regular spiking (RS) neuron ($a = 0.02, b = 0.2, c = -65, d = 8$) is to model the excitatory neuron and fast spiking (FS) neuron ($a = 0.1, b = 0.2, c = -65, d = 2$) is to model the inhibitory neuron, respectively. As shown in Fig. 2, both the RS and FS neurons fire very regularly when they are driven by a low suprathreshold direct current. However, when the stimulus is strong enough, they can fire burst. In addition, no matter when the membrane potential reaches a threshold $V_{th} = 30$ mV, the membrane potential and recovery variable are reset according to Eq. (3) after an action potential is generated. The noise current $I_i^{noise} = \sqrt{2D}\xi_i(t)$ represents the external or intrinsic fluctuations of the neuron itself, where the additive spatiotemporal Gaussian white noise $\xi_i(t)$ satisfies zero mean and unit variance, and D is referred to as the noise intensity. I_i^{syn} denoting the total synaptic current is the linear sum of the all incoming chemical synaptic current onto neuron i from neuron j, which has the form $I_i^{syn} = \sum I_{ij}^{syn}$, where $I_{ij}^{syn}(t) = g_{ij} r_j (E_s - v_i(t))$, g_{ij} describes the coupling strength of the synapse from neuron j to neuron i. Assume that the coupling strength is identical for all connections for simplicity. E_s represents the reversal potential which determines the type of synapse. $E_s = 0$ mV for excitatory synapse and $E_s = -80$ mV for inhibitory synapse. According to Ref. [48], excitatory or inhibitory synapses are determined by the types of pre-synapse neuron. Excitatory neurons always transmit the excitatory neurotransmitter to the post-synapse neuron and inhibitory neurons always transmit the inhibitory neurotransmitter to the post-synapse neuron, respectively. Here, the synapse variable r_j is the fraction of post-synaptically bound neurotransmitter obeying the first-order kinetics as follows:

$$\frac{dr_j}{dt} = \frac{1 - r_j}{1 + e^{-(v_j - \tau)}} - \frac{r_j}{10} \tag{4}$$

where τ represents the delay length. Moreover, I_i^{ext} is the external applied current. In the interest of ensuring the exhibition of the stochastic resonance in the FFL neuronal network motifs, we set $I_2^{ext} = I_3^{ext} = 2$ and consider that neuron 1 is subject to a local subthreshold periodic forcing, which is $I_1^{ext} = 2 + \sin(\omega t)$, where ω is the frequency of the weak signal. In the absence of noise, the external applied currents are too weak to excite the FFLs.

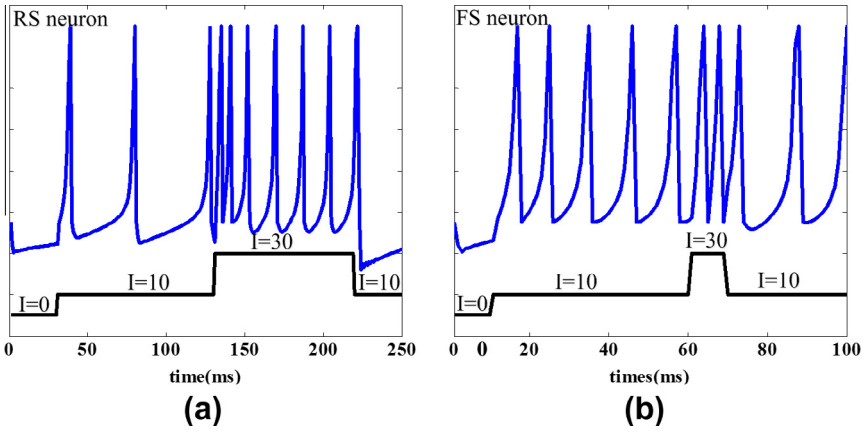

Fig. 2. Voltage responses of the Izhikevich neuron to the external current I: (a) regular spiking (RS) neuron and (b) fast spiking (FS) neuron.

In order to quantitatively characterize the correlation of temporal output series of output-unit v_3 with the frequency of the periodic subthreshold signal $\sin(\omega t)$, we calculate the Fourier coefficients Q for the input frequency ω, which is defined as

$$\begin{aligned} Q_{\sin} &= \frac{\omega}{2n\pi}\int_0^{\frac{2n\pi}{\omega}} 2v_3(t)\sin(\omega t)dt \\ Q_{\cos} &= \frac{\omega}{2n\pi}\int_0^{\frac{2n\pi}{\omega}} 2v_3(t)\cos(\omega t)dt \\ Q &= \sqrt{Q_{\sin}^2 + Q_{\cos}^2} \end{aligned} \tag{5}$$

where n is the number of period $2\pi/\omega$ covered by the integration time. The maximum of Q shows the best phase synchronization between weak input signal and output-neuron firing. In this paper, Q parameter is used to instead of the power spectrum because of the importance in the transport of the information encoded in the frequency ω, where Q parameter is a much more compact tool than the power spectrum [9,49].

3. Results

Since the value of Q is too low when neuron 1 is inhibitory, we only find interesting results for the FFL motifs with excitatory input neuron. The corresponding simulation results are shown in this section. Firstly, in order to investigate the role of the coupling strength, the time series of the input and output neuron in the case of different coupling strengths are shown in Fig. 3. It is shown that a spike from the input neuron induces both intermediate neuron and output neuron to respond. In Fig. 3(a), the neuron 3 couldn't respond every spike from neuron 1 because of the weak coupling strength $g = 0.15$. However, with the coupling strength increasing to 0.3, as shown in the Fig. 3(b), the output neuron could be driven to spike accurately. For the T1-FFL motif, in the case of coupling strength continued increasing ($g = 0.5$), because the intermediate neuron is excitatory, the output neuron may draw support from noise to fire burst which is very irregular and sparse due to its not

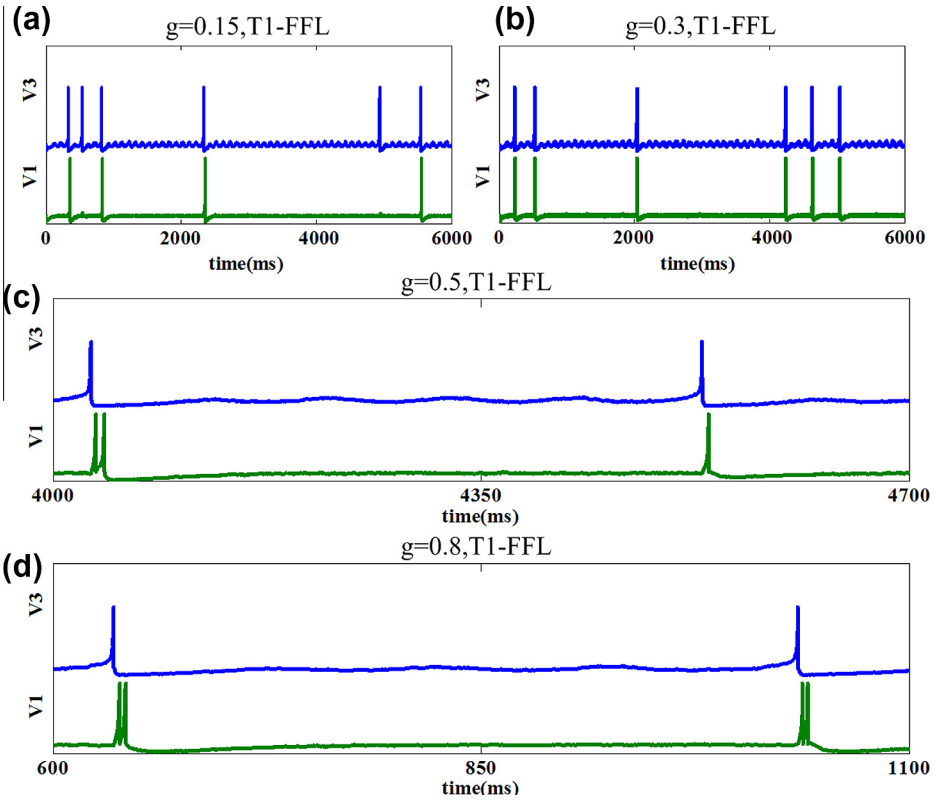

Fig. 3. Time series of the input and output neurons for different coupling strengths for T1-FFL motif: (a) when the coupling strength $g = 0.15$, the neuron 3 couldn't respond every spike from neuron 1; (b) when the coupling strength increases to $g = 0.3$, the neuron 3 could respond every spike from neuron 1 accurately; (c) when the coupling strength increases to $g = 0.5$, the output neuron may fire burst which is very irregular and sparse; (d) when the coupling strength increases continued to $g = 0.8$, the output neuron may fire regular burst. Noise intensity $D = 1.08$ and the frequency of the weak information $\omega = 62.8$ rad/s in all cases.

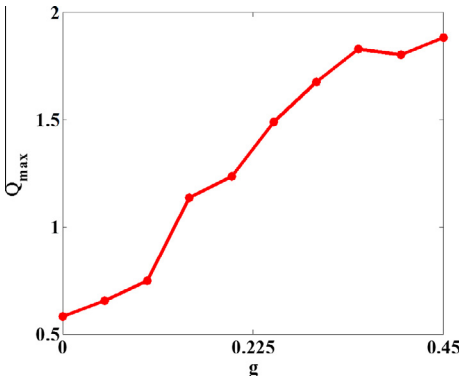

Fig. 4. The maximum of Q as a function of the coupling strength for both the T1-FFL motif. When the coupling strength $g > 0.3$, the maximums of Q maintain an almost constant level.

strong enough coupling strength as shown in Fig. 3(c). However, it's worth noting that when the coupling strength becomes large enough such as $g = 0.8$ in Fig. 3(d), the burst firing of the output neuron turns regular.

To further investigate the impact of coupling strength for the T1-FFL motif, the maximums of Q are calculated at the corresponding optimal noise intensities for different values of g as shown in Fig. 4. It is found that when the coupling strength $g > 0.3$, the maximums of Q maintain an almost constant level. This phenomenon results from the fact that increasing coupling strength just enhances the intra-bursting spikes. Thus, strong coupling strength couldn't destroy information propagation between the input and output neurons so as to enable the values of Q_{max} remain stable.

It was recently reported that different information transmission delays could induce stochastic resonance appear intermittently. For different coupling strengths, the Fourier coefficients Q are calculated as defined by Eq. (5), as the delay is varied. Numerical results in Fig. 5 shows the dependence of Q on the delay τ for different g. It can be found that in Fig. 5(a), for the T1-FFL motif, certain values of time delay τ significantly facilitate stochastic resonance in the case of the excitatory intermediate neuron. Here, the frequency of the weak period signal is set to 10 Hz. Interestingly, when time delay is up to exactly 100 ms, the stochastic resonance is enhanced. Notably, the second even the third harmonics of the intrinsic oscillations given by $\tau = 200$ ms and 300 ms can also result in a substantially lower peak of Q. Furthermore, for different coupling strengths, the intermittent appearance of stochastic resonance may not emerge obviously in the case of the small value of g. And for the large coupling strength, this phenomenon of the intermittent stochastic resonance could not change with the g further increasing. However, for the T2-FFL motif, due to its inhibitory intermediate neuron, large coupling strength could not induce the burst firing. Thus, time delay has little effect on the stochastic resonance with the help of the optimal external noisy intensity. Only slight perturbations emerge as the time delay varied as shown in Fig. 5(b). It is noteworthy that for the T2-FFL motif, because its inhibitory intermediate neuron could not transmit any extra information to output in the form of bursting, here the value of τ for the inhibitory neuron has no impact on the final simulation results. We can set the value

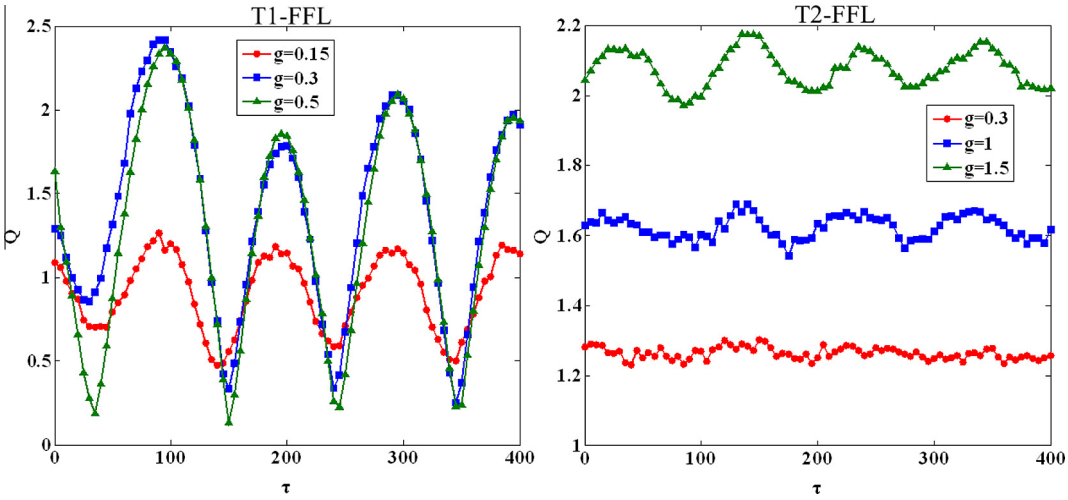

Fig. 5. Dependence of Q on the information transmission delays τ for different coupling strengths g. (a) T1-FFL motif (b) T2-FFL motif. The intermittent appearance of stochastic resonance may emerge obviously in the case of T1-FFL motif. Similar phenomenon couldn't appear in the T2-FFL motif.

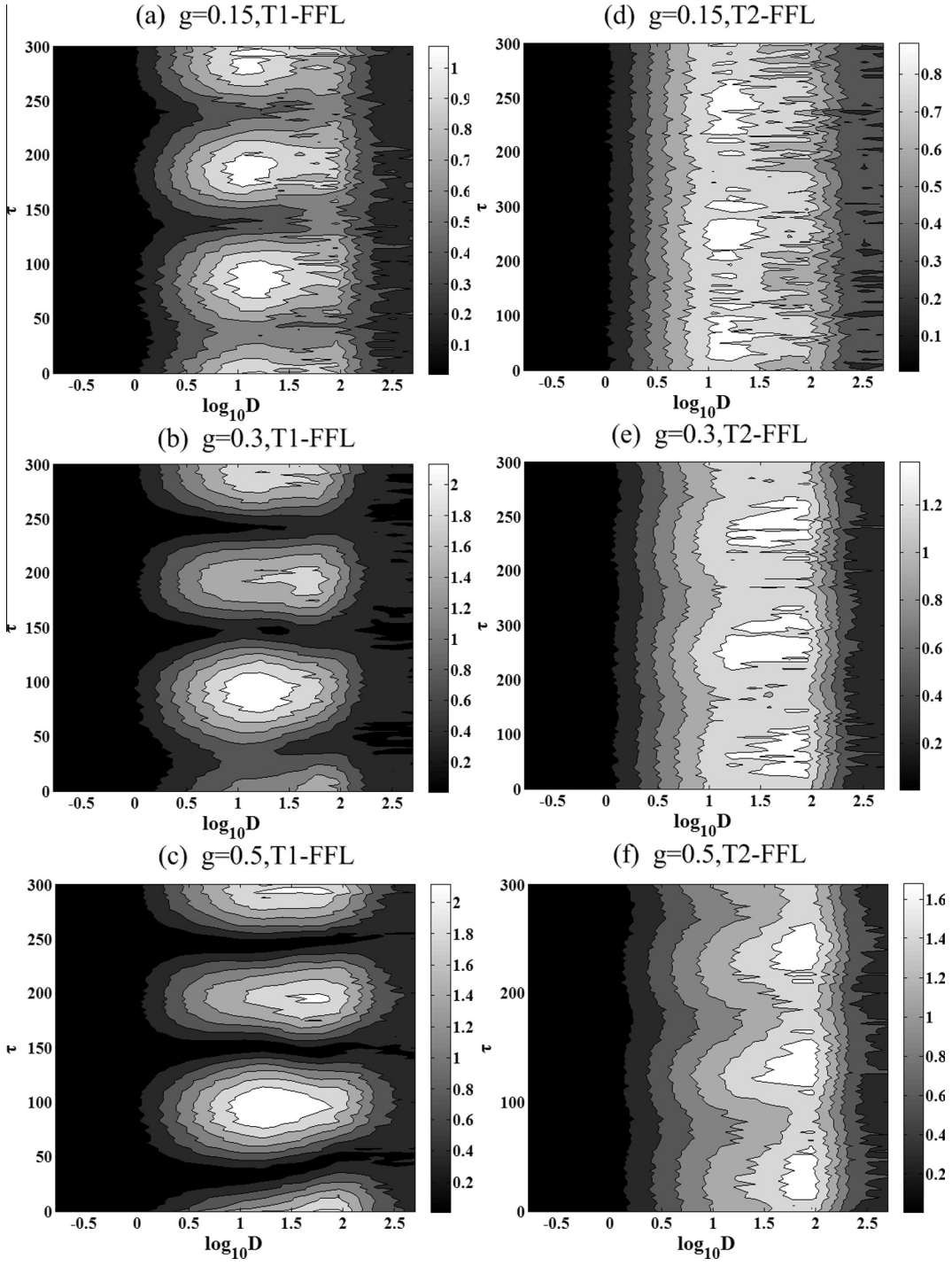

Fig. 6. The effects of the intermittent stochastic resonance Q both on noise intensity D and information tine delay τ for different coupling strengths in (a)–(c) T1-FFL motif and (d)–(f) T2-FFL motif. With the information transmission delay increasing, T1-FFL motif exhibits intermittent appearance of stochastic resonance for certain optimal noise intensity, whereas for T2-FFL motif this phenomenon doesn't emerge.

of τ randomly, which could not change the emergency of the tiny perturbations of the plots of Q. Whereas, the time delay τ for the excitatory neuron becomes the focus to induce the intermittent stochastic resonance. Furthermore, for the T4-FFL motif, the same situation will appear. It results from only the input neuron being the excitatory one.

To make an overall inspection, the dependence of Q on both noise intensity D and time delay τ is presented in Fig. 6(a)–(c) for T1-FFL motif and (d)–(f) for T2-FFL motif respectively. Indeed, it can be observed that there exist some bright circle-like

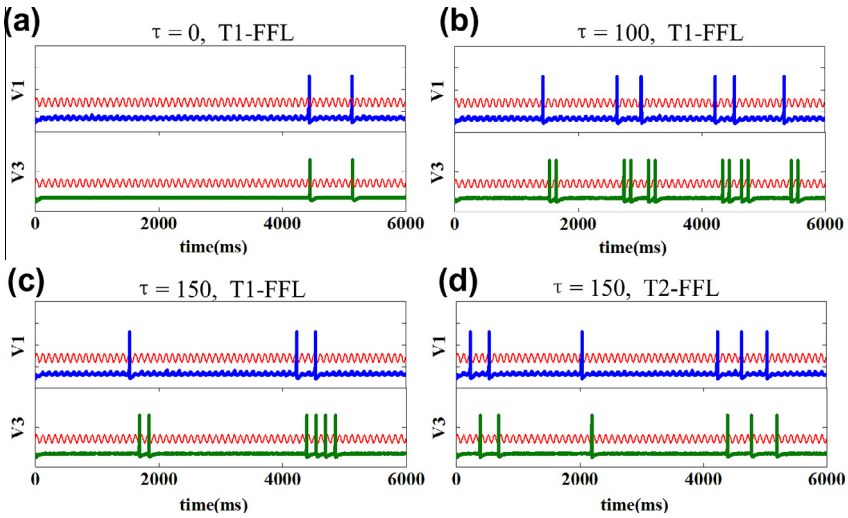

Fig. 7. Time series of the input and output neurons for different information time delays: (a) $\tau = 0$, T1-FFL; (b) $\tau = 100$, T1-FFL; (c) $\tau = 150$, T1-FFL; (d) $\tau = 100$, T2-FFL; Noise intensity $D = 1.08$ and the frequency of the weak information $\omega = 62.8$ rad/s in all cases.

regions of high values of Q, where stochastic resonance can be realized. With the information transmission delay increasing, T1-FFL motif exhibits intermittent appearance of stochastic resonance for certain optimal noise intensity, whereas for T2-FFL motif this phenomenon doesn't emerge. Moreover, from the color bar beside its own figure, the values of the maximum of Q are smaller in the T2-FFL motif than the ones in the T1-FFL motif. This implies the existences of the inhibitory intermediate neuron not only reduce the trends of the intermittent stochastic resonance, but also decrease the amplitude of Q_{max}. The results are similar to delay-induce multiple stochastic resonances in the scale-free neuron network [36]. Delay-induced stochastic resonances of neuronal activity result from the locking between the delay length and the global-resonant oscillation period of individual neurons if the latter is close to the oscillation period of the pacemaker.

In order to further explain the underlying mechanism of the intermittent stochastic resonance, Fig. 7 shows some certain delay-induced time series. Due to an excitatory intermediate neuron existing in the T1-FFL motif, information will propagate from two different transduction pathways. Specifically, the weak information can transmit from neuron 1 to neuron 3 directly, or via neuron 2. Thus for instance, if the time delay is 100 ms, the output neuron will fire a first spike 100 ms later than the input neuron resulting from the information propagation from the direct passage, and then another 100 ms delay, the output neuron will fire a second spike owing to the information propagation from the indirect pathway, as shown in the Fig. 7(b). By the way, Fig. 7(a) shows the situation of the no delay existing. Moreover, by comparing the time series in Fig. 7(c) and (b), the 150 ms time delay will make the interval of the adjacent spikes is also 150 ms causing the spike moments turn to be inconsistent, which is a reason that stochastic resonance disappears intermittently. However, for the T2-FFL motif, the intermediate neuron is inhibitory. Interesting findings are shown in the comparison between Fig. 7(c) and (d), implying that

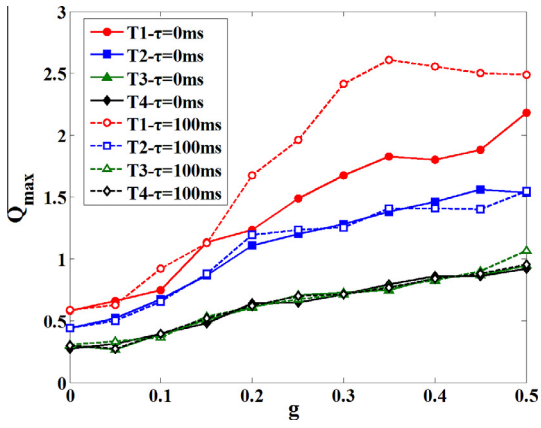

Fig. 8. The maximum of Q as a function of the coupling strength for the former four motifs in the case of no time delay and 100 ms time delay in the motifs respectively.

the inhibitory intermediate neuron couldn't promote the information propagation. Thus, the information can only transmit through the direct pathway causing disappearance of the intermittent stochastic resonance phenomenon.

Finally, to further investigate the influence of motifs' structures, the maximums of Q are calculated at the corresponding optimal noise intensities with the various coupling strength g for all four types of motifs. Presence or not of the certain time delay $\tau = 100$ ms also plays an important role, especially in the T1-FFL motif. It is found that the intermediate neuron's role in this motif consisting of three neurons from the line above. The excitatory intermediate neuron could induce intermittent stochastic resonance whereas the inhibitory ones weaken their influence on the intermittent mode. Nevertheless, it can be seen that Q_{max} for T1-FFL are always larger than the other motifs whether 100 ms delay exists or not in Fig. 8. This may result from the impact of the inhibitory neuron on the stochastic resonance in the other three types of the motifs. Moreover, it is obvious that if the motifs have the inhibitory output neuron, the effects of stochastic resonance are worse than the excitatory ones in the first two types of the motifs. More interestingly, in the regions of the coupling strength $g < 0.5$, where no burst firings emerge, time delay offers a large degree of enhancing the effect of the stochastic resonance, especially in the case of all excitatory neurons.

4. Discussions and conclusions

The intrinsic complexity of the complex networks brings us the difficulties to study them as a whole. Network motifs as some significantly recurring nontrivial patterns of interconnections are becoming the hot spots providing us a new way to study complex networks. Thus, elucidating these motifs' dynamics and functions for different structures would shed light on the whole networks' behaviors. In the present work, time delay-induced intermittent stochastic resonance in the FFL neuronal network motifs is studied via computational modeling. Using Izhikevich neuron differential equations and the chemical synapse to describe the FFL motifs' structures and features, we built the stochastic models to make a detailed investigation on the time delay induce the stochastic resonance. Depending on whether the neurons in the FFL motifs are excitatory or inhibitory, eight possible structural configurations of the FFLs have been discussed. Numerical results obtained from the study of stochastic resonance show that only four FFL types where the input neuron is excitatory can obtain high values of Q at optimal noise intensities and large coupling strengths. Especially, by comparing the Q at corresponding coupling strength, it was found that due to the all excitatory neurons in the T1-FFL, the effect of the stochastic resonance is better than the other types. Large coupling strength in the motifs can promote the stochastic resonance; in particular, for T1-FFL motif large coupling strength may cause bursting.

Since the FFL motifs exist widely in real neuronal networks, besides the influence of the ubiquitous noise, time delay may have a significant impact on the stochastic resonance. For T1-FFL and T3-FFL motifs, excitatory intermediate neuron brings a second indirect pathway of the information propagation. Thus, a very interesting phenomenon exists that stochastic resonance appears intermittently. However, due to the difference between the intermediate neuron, inhibitory intermediate neuron for T2-FFL and T4-FFL could not exhibit the similar intermittent phenomenon. More interestingly, for the excitatory intermediate neuron, when the time delay is just equal to the period of the weak information, these kinds of motifs could exhibit the best effect of the stochastic resonance. In addition, the type of the output neuron plays an important role in the stochastic resonance. Excitatory output neurons in the T1-FFL and T2-FFL could enhance the effect of the stochastic resonance whereas the inhibitory ones in the T3-FFL and T4-FFL may decrease the maximum values of the Q.

Since realistic neuronal networks contain a great number of the FFL motifs, and noise and delay are ubiquitous in neural systems, the noise-induced dynamic behaviors presented in this paper may have some biological implications, especially simplification for the studying of the complex neuronal networks. Further works on this research field include studying other neuronal network motifs, such as the motifs consisting of four neurons and with electrical and chemical hybrid synapse in order to provide some insights into the neural information transmission mechanism of the FFL neuronal network motifs.

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